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REVIEW

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A history of research on arbuscular mycorrhiza

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Abstract This is not a review paper in the traditional sense, of which there are many. Three of the most influential reviews that summarized well some of the "older" literature include those by Nicolson (1967), Gerdemann (1968) and Mosse (1973). Instead, in this brief and incomplete work, we attempt to show the historical development of research on arbuscular mycorrhizas. We owe much to those who have written other historical accounts, including Rayner (1926–1927), Trappe and Berch (1985), Mosse (1985), Schenck (1985), Harley (1991) and Allen (1996), but the contents of this work naturally reflect our own ignorance, interests and biases. It was often difficult to distinguish between the historical and the contemporary, and we did not use any specific cutoff date in making this distinction. The degree to which we include "contemporary" literature was determined by our own assessment of its connectedness to older literature. In any case, we hope this will be of some interest to those of you who study the arbuscular mycorrhiza, and that it will serve the purpose of providing what we consider to be an important historical context for current researchers. We wish you good fortune in your research.

Keywords Arbuscular mycorrhiza · Discovery · Nomenclature · Physiology · Plant productivity

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Introduction

Today, mycologists and plant scientists are typically well versed in the function of arbuscular mycorrhizas and their consequences for nutrient cycling and plant productivity. It would be difficult to attend mycology, botany or ecology meetings without hearing about this symbiosis. Thus many researchers in our field, particularly younger researchers, may be surprised to learn that experimental studies of the arbuscular mycorrhiza are actually rather new. A short while ago the existence of arbuscular mycorrhizas was not even widely appreciated, and initially they were not highly regarded. Because of their rather controversial linkage to the beneficial effects of composting in India (Howard 1940) they came to be known as the "mal aimée des microbiologistes" (Bertrand 1972). As evidence of the newness of their study, we call attention to Harley's second edition of *The Biology of Mycorrhiza* (Harley 1969). Among the very last words in that work were: "The study of phycomycetous endotrophic mycorrhizas is therefore seen to have emerged as a reputable pursuit". How is it possible that this field of research had only become "reputable" 35 years ago, 127 years after what is considered by some to be the first description of an arbuscular mycorrhiza (Nägeli 1842)? The answer to that question is simple. The identity of the fungi involved and their effects on plants remained a matter of conjecture for many, many years! This was in large measure because of the obligate symbiotic nature of arbuscular mycorrhizal fungi. Despite this large impediment to arbuscular mycorrhiza research, there is now a general appreciation for the agricultural and ecological relevance of the symbiosis. This is the legacy of a relatively small community of committed researchers, who worked largely apart from the mainstream of biological investigation not so long ago.

Discovery and description

Arbuscular mycorrhizas may have been described as early as 1842 (Nägeli 1842), but most of Nägeli's drawings only remotely resemble the arbuscular mycorrhiza. Trappe and Berch (1985) and Rayner (1926–1927) cite other early observations of the symbiosis during the period 1875–1895. Extensive surveys of host plants and sophisticated anatomical descriptions of what are most certainly arbuscular mycorrhizas are given by Schlicht (1889), Dangeard (1896), Janse (1897), Petri (1903) Gallaud (1905), Peyronel (1924), Jones (1924) and Lohman (1927). As early as 1889, Schlicht had already observed the basic anatomical relationships between host and fungal tissues. Janse (1897) called the intramatrical spores "vésicules" and determined that other structures, named "arbuscules" by Gallaud (1905), were located in the inner cortex. Gallaud (1905) made very accurate observations of the arbuscule and concluded, for example, that it is entirely surrounded by a host membrane, which was later confirmed by Cox and Sanders (1974) using transmission electron microscopy. Gallaud (1905) also noted that partial digestion of the arbuscule resulted in a structure called the "sporangiole" by Janse (1897); this observation was confirmed by electron microscopy years later (Cox and Sanders 1974). Gallaud (1905) further distinguished between *Arum* and *Paris* types of arbuscules (Smith and Smith 1997). Jones (1924) described the appresorium. Light and electron microscopical studies of arbuscular mycorrhizas were facilitated by the founding in 1950 of the Centro di Studio sulla Micologia del Terreno by Peyronel in Torino, Italy (Bonfante 1991). There, Scannerini and Bellando (1968) first noted that a space between the host membrane and the fungal wall contained materials of host origin, probably unconsolidated components of host cell wall.

Early researchers used classical methods of cutting and staining sections of paraffin-embedded roots to produce excellent drawings and photographs of the arbuscular mycorrhiza. Alternatively, very good photographs have been obtained by cutting sections of fresh roots on a freezing microtome. However, both methods are laborious if mycorrhization is to be quantified. The problem was largely solved by clearing the roots of cytoplasm by heating in KOH and staining fungal cell walls with trypan blue in lactophenol (Phillips and Hayman 1970). The Phillips and Hayman paper is probably among the most frequently cited of all papers dealing with arbuscular mycorrhiza, but the use of hot KOH as a clearing agent was by no means new, having already been used by Janse (1897), Peyronel (1940) and Bevege (1968). There are now other methods of staining, but the basic procedure of using KOH to remove host cytoplasm is common to nearly all. Although there were some notable reports of the widespread nature of arbuscular mycorrhizas prior to the 1970 publication of Phillips and Hayman (Janse 1897; Gallaud 1905; Jones 1924; Lohman 1927), the arbuscular mycorrhizal fungi were still considered by most to be rare. With the broad application of clearing and staining, however, arbuscular mycorrhizas were more readily documented in abundance in many habitats (Read et al. 1976 and references therein). Quantification of mycorrhization has been achieved in various ways. Many early studies simply cut root systems into small pieces and determined the proportion of the pieces that were mycorrhizal. Probably the most popular method today is based on the line intersect technique devised by Newman (1966), which was possibly first applied to mycorrhizas in 1975 (Sparling and Tinker 1975). Giovannetti and Mosse (1980) later compared various methods of mycorrhiza quantification, which led to greater acceptance of the line intersect method. Mycorrhizas are complex symbioses and the fungi involved produce a variety of structures within the root. Quantification of these structures (hyphae, arbuscules, vesicles) was standardized by the method proposed by McGonigle et al. (1990).

Although there were already many independent descriptions of the arbuscular mycorrhiza in the late 1800s and early 1900s, the true identity of the fungi involved remained unknown for many decades. So unclear was their identity that at one point the possibility was circulated that a single fungus could form both ectomycorrhizas and arbuscular mycorrhizas (Lohman 1927). The inability to properly identify a fungus as being arbuscular mycorrhizal was caused in large measure by the inability to independently culture any of them. The classical way to identify an agent of disease (and, by extension, the fungi responsible for the mycorrhizal symbiosis) is to apply Koch's postulate, and one of the necessary steps is the isolation and culture of the organism involved. From the earliest days there appear to have been attempts to independently culture arbuscular mycorrhizal fungi. Janse failed, as did Gallaud (Rayner 1926–1927), Peyronel (Harley 1991) and Jones (1924). Often, researchers attempted to use standard nutrient media, or standard media amended with some "vital component". Magrou (1946), working in France, observed fungal growth from cut ends of intramatrical hyphae in pieces of surface-sterilized potato roots in hanging drop cultures. The emerging hyphae grew quite vigorously but they could not be subcultured. Their growth stopped when the supporting root piece became moribund. Stahl (1949), in Germany, found that the arbuscular mycorrhizal fungus could grow 10 cm across sterile sand if it remained attached to a living host, but she too failed at its independent culture.

Between 1952 and 1957 a fungus first isolated by Nicholls (1952) from surface-sterilized mycorrhizal onion roots was identified as a strain of *Pythium ultimum*. In 1955 Harrison, also from the Bristol group, isolated this organism again using the hanging drop technique of Magrou. Experiments to test whether inoculation with such isolates could produce typical arbuscular mycorrhizas were summarized by Hawker et al. (1957). The abstract of that paper reads "Inoculation with the isolates of *Pythium ultimum*, under certain conditions led to development of typical hyphae and vesicles within the root and, in older seedlings, to formation of the characteristic arbuscules." However, this observation was made on roots from open pot cultures, which are subject to soil contamination from adjacent pots.

In 1961 Barrett reported the isolation and culture of fungi from arbuscular mycorrhizal roots via a transitional stage of growth on pieces of hemp seed. He called the fungus *Rhizophagus* and claimed that it produced arbuscular mycorrhizas in other test plants. Re-isolation of the fungus from such plants again required the transitional hemp seed phase. Mosse (1961) once obtained arbuscular mycorrhizas by inoculating a few plants with this fungus in an open pot experiment maintained for a long time, but subsequent tests with better-protected plants failed (Mosse 1963). Gerdemann (1971) was unable to culture the fungus using the hemp seed technique.

Because the arbuscular mycorrhizal fungi could not be cultured, their identities as the fungi responsible for the arbuscular mycorrhizal symbiosis had to be established in other ways. In the 1920s and 1930s Peyronel (1923, 1924, 1937) traced the hyphae from mycorrhizas to spores of *Endogone fuegiana*, *Endogone vesiculifera* and another *Endogone* species. He also advanced the notion that the typical syndrome of arbuscular mycorrhiza was due to a dual infection by a *Rhizoctonia* and an *Endogone*, and this was widely believed at the time. However, he did not test to see if inoculation with any particular fungus resulted in a typical arbuscular mycorrhiza. This was not to happen until Mosse's first successful "vesicular-arbuscular mycorrhizal infection" of strawberry (Mosse 1953) using nonsterile sporocarps of a fungus initially named *Endogone mosseae* in her honor (Nicolson and Gerdemann 1968), which later became *Glomus mosseae*. Incidentally, Mosse's 1953 publication describing her landmark research consisted of three very brief paragraphs!

Inoculation with surface-sterilized sporocarps associated with mycorrhizal strawberry roots also produced mycorrhiza in apple, wheat, various grasses, tomato and lettuce in open pot experiments, demonstrating its wide host range (Mosse 1956). Gerdemann (1955a) also showed that spores from his "type B" isolate, later named *Gigaspora gigantea,* had a wide host range and could successfully form arbuscular mycorrhizas with several species of plants including red clover, maize, strawberry and sweet clover. The experiments of Gerdemann and Mosse thus well established the absence of a strict host-specificity by at least some arbuscular mycorrhizal fungi, and together provided evidence that arbuscular mycorrhizas could be caused by more than one species of fungus. Gerdemann (1955a) was careful to note that the mycorrhiza from his "type B" spores was arbuscular and that no vesicles were produced, which distinguished his fungus from the one used by Mosse. It thus became clear that there were at least two patterns of symbiotic development by arbuscular mycorrhizal fungi.

The giving of names

Frank (1885) gave the name "mycorhiza" to the peculiar association between tree roots and ectomycorrhizal fungi. A thorough discussion of the derivation of the word "mycorrhiza", including the incorporation of the second r is given by Kelley (1931, 1950). In another publication, Frank (1887) recognized a distinction between ectotrophic and endotrophic mycorrhizas, which included at the time only ericaceous and orchid mycorrhizas. The name for the arbuscular mycorrhizal symbiosis has changed through the years. The symbiosis was once frequently called "phycomycetous endomycorrhiza" to distinguish it from the endomycorrhizal symbioses formed between members of the Ericaceae or Orchidaceae and higher fungi. The name "Phycomycete", however, no longer carries any systematic significance. As previously mentioned, Janse (1897) called the intramatrical spores "vésicules" and Gallaud (1905) called the other commonly observed intracellular structures "arbuscules". Thus the name "vesicular-arbuscular mycorrhiza" was established and persisted until recently. The recognition that not all fungi formed vesicles led to the proposal that this symbiosis should be renamed arbuscular mycorrhiza. This change is now widely accepted, but in some of these associations the fungi may not even produce proper arbuscules (Smith and Smith 1997). Moreover, one must agree that some hosts of arbuscular mycorrhizal fungi do not house the fungi in true roots at all, and therefore that the name "mycorrhiza" is not correctly used in those cases (Lohman 1927; Kelley 1931). If we continue with the line of reasoning that dropped the "vesicular" from the "vesicular-arbuscular mycorrhiza", we must also drop the "arbuscular" and, if we wish to be more inclusive of associations involving these fungi, we must also drop the "-rhiza". We would then be left only with "myco-" and that is useless. Perhaps "phycomycetous endomycorrhiza" was not such a bad choice after all. We are having fun here, of course, but it is interesting to note the continual problem we have had with names. Although it is no laughing matter, one might be amused to count the times we have questioned what should even be considered a mycorrhiza in the first place (Boullard 1982; Allen 1996; Trappe 1996; Jones and Smith 2003; Massicotte and Peterson 2003)!

The naming of organisms and the establishment of their evolutionary relationships are of great importance in any field of biology. At the 1974 Leeds meeting (Sanders et al. 1975), the name *Endogone* was used by many in attendance to describe the "phycomycetous endomycorrhizal" fungi. Another outdated name for arbuscular mycorrhizal fungi, *Rhizophagus*, was also in use at the time and continued to be used until about 1977. Thus, as recently as 25 years ago the nomenclature of the arbuscular mycorrhiza fungi had not been firmly established.

The history of the naming of our fungi is certainly an interesting one. Link (1809, cited in Gerdemann 1971), established the genus *Endogone*. Tulasne and Tulasne (1844) were the first to describe the genus *Glomus*, known only from spore clusters found in the soil. No connection to the mycorrhizal symbiosis had yet been suggested. The Tulasne brothers considered *Glomus* to be closely related to *Endogone*. Fries (1849) established the Endogonaceae, placing it in the Tuberales, but the family was transferred to the Mucorales by Bucholtz (1912). Dangeard (1896) was the first to describe an arbuscular mycorrhiza, which happened to have formed from poplar roots. He regarded this as a disease and named the fungus *Rhizophagus populinus* (Dangeard 1900), provisionally placing it within the Chytridiales. In 1922 Thaxter revised the Endogonaceae, placing the *Glomus* of Tulasne and Tulasne into *Endogone*. He considered *Endogone* to contain both zygosporic (notably *Endogone lactiflua*) and chlamydosporic species, observing that at least one species apparently produced both kinds of spores. In 1939 Butler, in reviewing the identity of arbuscular mycorrhizal fungi, classified them as probable imperfect members of the Endogonaceae. He nevertheless accepted the name *Rhizophagus* for such fungi because of the earlier naming by Dangeard.

The extraction of spores from soil is necessary for their classification. Routine extraction from soil was made possible by wet sieving and decanting, a method commonly used to extract nematodes from soil and adapted to arbuscular mycorrhizal fungi by Gerdemann (Gerdemann 1955a; Gerdemann and Nicolson 1963). Mosse (1953), Gerdemann (1955a, 1961, 1965) and Gerdemann and Nicolson (1962, 1963) added more species to Peyronel's (1924, 1937) existing list of *Endogone,* whose spores could produce typical arbuscular mycorrhizas. Gilmore (1968) further added to the list by describing six spore types, E_2–E_7, found in pot cultures. All these "species" based on spore type seem to have little in common except that they produced aseptate multinuclear hyphae, extramatrical spores, intracellular arbuscules or hyphal coils, and could not be cultured. At this point it seemed time to attempt some classification or method of recognition of all arbuscular mycorrhizal spore types. Nicolson and Gerdemann, both plant pathologists by training, decided on the classical system with Latin names. Mosse (a plant anatomist) and Bowen (an ecologist) attempted a more descriptive system based mainly on spore wall structure and color, and cytoplasmic characteristics (Mosse and Bowen 1968). Nicolson and Gerdemann (1968) divided the fungi into two groups of *Endogone*, one forming extramatrical azygospores/zygospores arising from the tip of a swollen hyphal suspensor but producing no intramatrical vesicles, corresponding to the bulbous vacuolate and bulbous reticulate types of Mosse and Bowen (1968), and the other forming extramatrical chlamydospores and intramatrical vesicles corresponding to the yellow vacuolate and red brown laminate spores of Mosse and Bowen (1968). There was thus some correspondence between the two attempts at classification. Because spores possessed so few distinguishing features, which were frequently affected by age and environment, the naming of new species became quite a popular pursuit, but the E_3 type of Gilmore, which is quite common in nature, did not and has not since found a home anywhere.

In the early 1970s it became clear to Gerdemann and Trappe (Gerdemann and Trappe 1974) that Endogone, which now contained a wide variety of species, needed further revision. They split the old *Endogone sensu lato* into seven genera including *Endogone*, *Modicella*, *Glaziella* (nonmycorrhizal genera), and four mycorrhizal genera including *Glomus* (which they resurrected, and which had also previously been referred to as *Rhizophagus*), a previously described mycorrhizal genus, *Sclerocystis*, and two new genera *Gigaspora* and *Acaulospora*, which corresponded to the honey-colored sessile spores of Mosse and Bowen (1968). These were all placed in the Endogonaceae, Endogonales, Zygomycetes.

Trappe and Schenck (1982) recognized another mycorrhizal genus, *Entrophospora*. In 1987, Walker also recognized five arbuscular mycorrhizal fungal genera, having dropped *Sclerocystis* and added *Scutellospora*. In 1990, Morton and Benny placed the five genera of Walker (1987) into three families (Glomaceae, Acaulosporaceae, Gigasporaceae) and two suborders (the Glomineae and the Gigasporineae), both of which were then placed in a new order, the Glomales. Later, Morton and Benny (2001) recognized two other families, the Archaeosporaceae and Paraglomaceae, with two new genera, *Archaeospora* and *Paraglomus*.

In 2001 Schüßler et al. used molecular data to establish the relationships among arbuscular mycorrhizal fungi and between arbuscular mycorrhizal fungi and other fungi. The group of arbuscular mycorrhizal fungi was elevated to the level of phylum (Glomeromycota), which was shown to be as distinct from other fungi as the Ascomycota are from the Basidiomycota. Little did the early researchers know that they were studying an entirely new phylum of fungi! The Zygomycota were shown to be polyphyletic, and *Endogone* did not group near the Glomeromycota nor did it group with the Mucorales. *Geosyphon pyriforme* was added to the Glomeromycota, which may have far reaching effects on our understanding of the arbuscular mycorrhizal symbiosis.

The effect of continual revision of the taxonomy of the fungi had an exasperating effect on many colleagues not directly concerned with the taxonomy. Schenck (1985) was sensitive to this issue and gave voice to the concerns of many at the 6th North American Conference on Mycorrhizae. His comments about this make amusing reading.

The methods employed by taxonomists have become increasingly sophisticated. Initially, of course, taxonomies were based upon morphological and anatomical characteristics of the fungi. Later, methods based on serology (Aldwell and Hall 1987), isozyme variation revealed by gel electrophoresis (Hepper 1987) and fatty acid variation (Bentivenga and Morton 1994) were introduced. Systematists have come to rely increasingly on DNA-based methods (Cummings 1990; Davidson and Geringer 1990; Simon et al. 1990, 1992, 1993; Redecker 2000). While DNA variation may be the best measure of genealogical relationships among organisms, it is amazing the extent to which anatomical and DNA-based methods have yielded similar results. Routine identification of arbuscular mycorrhizal fungi will probably continue to be based primarily on structural characters and thus an increased appreciation of the relationship between anatomy and DNA will be important.

The ability to properly name the fungi, avoid duplication of names and relate the species to one another depends heavily on collections such as those held by INVAM, the International Culture Collection of Arbuscular and Vesicular-arbuscular Mycorrhizal Fungi, and the BEG, International Bank for the Glomeromycota. Schenck created INVAM in 1985. Since 1990 the collection has been curated by Morton at West Virginia University (http://invam.caf.wvu.edu/). The BEG/IBG is an international collaborative effort that provides registration of individual isolates of fungi for research purposes (http://www.kent.ac.uk/bio/beg/). This will insure a higher degree of certainty of the identity of the fungi in use by researchers around the world.

Effects on host plant growth

For many years researchers only speculated about the effects of the fungi on plant growth. Naturally, most researchers tended to regard fungi infecting plant tissues as pathogens or parasites. The early name "Rhizophagus" (Dangeard 1900), literally "root eater", clearly reveals Dangeard's prejudice. While Rayner (1926–1927) conceded that ectomycorrhizal fungi might be beneficial to their hosts, she was not quite willing to state the same of arbuscular mycorrhizal fungi. She did say, however, that only experiments with mycorrhizal and nonmycorrhizal plants could establish the truth. This sentiment was echoed by Harley years later (see below). The table of contents of the article by Burges (1936) readily reveals that the "pathology" of the mycorrhiza was an important subject. A group of researchers (Jones 1924; O'Brien and MacNaughton 1928; Koch 1935; Hildebrand and Koch 1936) regarded them as pathogens or forerunners of disease in strawberries, tobacco, legumes and other plant species. These early assumptions are rather interesting because, with the notable exception of Jones (1924), most early observers did not note any sign of pathology in host tissues. Although Jones believed the fungi to be pathogenic, he also noted that the "...conspicuous vigor in these plants in any locality can hardly be ascribed to the absence of this fungus." The strongest evidence of parasitism may have been the rather rapid loss of integrity of the arbuscule or its "digestion" as it was referred to (Gallaud 1905). Arbuscular mycorrhizal fungi are biotrophic (see below), and carbon compounds may primarily flow from host to fungus via living arbuscules (Bécard and Piché 1989a). Thus, digestion of the arbuscules by the host does appear to be a method of restricting the degree of parasitism.

In any case, despite conjecture concerning the negative effects of arbuscular mycorrhizal fungi on plant growth, there were initially no experiments to determine their effects, which prompted Harley (1950) to write "Although much is known, therefore, of the incidence and appearance of vesicular-arbuscular mycorrhiza, we know little or nothing of the physiology of the association ... Until such information is obtained, speculation about the function of this type of mycorrhiza should be avoided." As far as we are aware, the first experimental demonstration of this occurred prior to this statement. Asai (1943) published a paper on this in Japan (written in a nearly unintelligible form of German) during World War II. Using nonsterile soil as an inoculum, Asai demonstrated that mycorrhizal plants grew faster than nonmycorrhizal plants. Initially, few researchers elsewhere in the world could have been aware of this work due to the unfortunate timing of its publication. When Asai's paper was discovered, some attributed the positive effects of inoculation on plant growth to microbial detoxification of heat-treated soil (Mosse 1985). Progress in the study of the function of the symbiosis was made in Europe in 1957, when Mosse published a report showing that arbuscular mycorrhizal infection led to improved growth of apple seedlings and clonal leaf bud cuttings. She used sporocarps of *Endogone (Glomus) mosseae* to inoculate plants growing in autoclaved soil. In 1958, Peuss showed that inoculation with mycorrhizal roots increased growth of tobacco growing in subsoil or in soil that had been fallow. In 1963 Clark, using surface-sterilized mycorrhizal roots as inoculum, reported an increase of growth of tulip poplar trees planted in fumigated soil, and Meloh (1961, 1963) showed that the growth of maize and oats could be improved by arbuscular mycorrhizal fungi. Gerdemann (1964) also demonstrated improved growth in maize. He grew plants in steamed soil, inoculating his test plants with sporocarps and his control plants with sporocarp washings, a technique that was to become the standard for introducing coexisting microorganisms into the control medium. It was probably these early observations of plant growth promotion that led to the great increase in popularity of arbuscular mycorrhiza research in the decade following. Further progress in understanding the effects of arbuscular mycorrhizal fungi on plant growth was made possible by producing large volumes of inoculum initiated from single isolates of fungal species produced in "pot cultures" (Nicolson 1967; Gerdemann 1971).

We must not leave the impression that arbuscular mycorrhizal fungi always cause plant growth increases. While variation in the nature of mycorrhizal effects on the host has been noted recently (Janos 1980; Johnson et al. 1997), the same concept had been suggested long ago by Lohman (1927). Thus, there are notable cases of growth depression apparently caused by arbuscular mycorrhizal fungi in "non-host" species (Francis and Read 1984) or in host species when phosphate availability is high (Mosse 1973; Peng et al. 1993) or in other cases (Modjo and Hendrix 1986). It seems, then, that early researchers claiming arbuscular mycorrhizal fungi to be parasites or pathogens may not have been entirely incorrect.

It is relevant here to discuss the terms "infection", "colonization" and "mycorrhization". For many years we referred to the association as an infection. A number of colleagues felt that the term was pejorative and implied a state of disease. Perhaps the term "infection" is simply left over from the early days when the association was assumed to be parasitic or pathogenic. "Colonization" was thus thought to be more accurate. However, others have used the term “mycorrhization” and we lean in this direction if a choice has to be made. “Mycorrhization” has the advantage of “colonization” in that it is neutral with respect to the effects on the host. Furthermore, “mycorrhization” is a single word that does not require the addition of “mycorrhizal” as in “mycorrhizal colonization”.

Nutrient uptake by the extramatrical mycelium

Initially the cause of the positive effects of arbuscular mycorrhizal fungi on plant growth was not known. For example, Mosse (1957) did not analyze her apple tissues for phosphorus (P) content. The suspicion from early on was that the fungi somehow increased nitrogen (N) uptake. Some felt that the fungi helped to breakdown soil organic matter as a source of N or, perhaps, that they fixed N (Lohman 1927). Rayner (1926–1927) wrote that “It is well to recall the fact that in the plant world, the severity of the struggle for existence not uncommonly centers about the competition for suitable compounds of nitrogen...On a priori grounds, it is not unreasonable to believe that the intimate association with fungus mycelium, so common in all groups of vascular plants and also in the thalloid members of the Bryophyta is but another manifestation of the urgency of this nitrogen problem among plants.”

In 1959 Baylis from New Zealand was, perhaps, the first to suggest that the beneficial mycorrhizal effect was mediated by P uptake. Mycorrhizal *Griselinia* seedlings grown in a P-deficient soil took up 3–5 times as much P as nonmycorrhizal seedlings. In 1964, Gerdemann also demonstrated that nonmycorrhizal plants exhibited “severe phosphorus deficiency symptoms” and had significantly lower P concentrations and higher K and Mg concentrations than mycorrhizal plants. Gray (1964) showed that mycorrhizal plants contained more P than nonmycorrhizal plants. Holevas (1966) further showed positive effects of mycorrhizal infection in P-deficient soil but not in soil to which additional P was added. Similar findings were reported by Daft and Nicolson (1966), Murdoch et al. (1967), Nicolson (1967) and Hayman and Mosse (1971).

In many other experiments with a range of plant species, researchers studied the effects of adding P in various amounts and of varying solubility on growth of mycorrhizal and nonmycorrhizal plants. Baylis, who mentored a notable second generation of arbuscular mycorrhiza researchers, studied the growth responses to mycorrhizal infection of five plant species at three levels of added P (Baylis 1970, 1972b). He concluded that the species fell into three groups according to their requirement of a minimum value of available P, below which they grew very little. He thought that this threshold value might relate to the extent of root-soil interface, and suggested that arbuscular mycorrhizal fungi and root hairs were essentially alternative mechanisms for plant P uptake. Probably unknown to him, this confirmed observations by Schlicht (1889) that plants with mycorrhiza flourished on nutrient-poor soils and that mycorrhizas were particularly prevalent in plant species with thick fleshy roots, few root hairs, or otherwise reduced root systems. Similar observations were made by five other authors between 1900 and 1923, and were summarized by Peyronel (1937): “Plants fall into two large groups according to their root development: those with thread-like very thin roots with long root hairs are rather sparsely mycorrhizal while still in the active living state and those with thick fleshy roots are usually strongly mycorrhizal.”

Baylis (1972a) emphasized that root hair length is a good predictor of benefit from mycorrhizal fungi. A refinement of this hypothesis was offered by Abbott and Robson (1984) and more formally by Koide (1991). They indicated that prediction of benefit from mycorrhizal fungi depends on both the supply of P, which is affected by root hair length, and the requirement for P, such as represented by the potential for plant growth. Thus, the extent to which the P requirement exceeds the P supply determines plant response.

Legumes have a relatively high P requirement for nodule development and nitrogen fixation. Asai (1944) was probably the first to point out that normal levels of nodulation may depend on the presence of mycorrhizal fungi. Asai’s early observations were confirmed and extended in numerous publications on a range of legumes (Crush 1974; Daft and El Giahmi 1974; Smith and Daft 1975; Mosse et al. 1976; Powell 1976; Barea et al. 1988).

Peyronel (1950, translated in Harley 1991) wrote that “...the development of the mycelium in these mycorrhizas is not at all limited to the cortex of the roots but extends in many filaments to the surrounding soil; this causes one to think that the endophyte, as well as modifying the osmotic and enzymic properties of the infected cells, can absorb from the soil at least a part of the principal nutrients necessary to the plant symbiote”. Thus, the extra P in mycorrhizal plants could be due either to an indirect mycorrhizal effect on root structure or physiology, or to direct uptake by hyphae with subsequent transfer to the root, or both (Sanders and Tinker 1973).

Early on, Sanders and Tinker (1973) reasoned that the hyphae took up and transferred P to the host because P inflow into mycorrhizal roots was substantially higher than in nonmycorrhizal roots, which was limited by diffusion. The distinction between indirect effects on the root and direct hyphal effects was made possible by spatial separation of colonised roots and extramatrical mycelium (Hattingh et al. 1973; Schüepp et al. 1987). The basic method of Schüepp et al. (1987), which employed fine meshes to separate root from hyphal compartments, subsequently led to many important observations, including the discovery that some fungal species mainly explore the soil immediately adjacent to the root, while others explore it more distantly (Jakobsen et al. 1992a, 1992b). The existence of such functional diversity among arbuscular mycorrhizal fungi suggests that a combination of several species of fungi could increase the effectiveness of phosphate extraction from the soil. The separation of fungal from root compartments also led to the discovery that the fungi can absorb the majority of P eventually acquired by the plant and, in some cases, the fungi perform virtually all of this function (Pearson and Jakobsen 1993; Smith et al. 2003)!

The extra P in mycorrhizal roots could be due either to better soil exploration by the extramatrical mycelium, or to the ability of the fungus to utilize or mobilize sources of soil P not available to plant roots. Following ^{32}P labeling of labile soil phosphate, the specific activities of P in mycorrhizal and nonmycorrhizal plants were not significantly different. This suggested that the primary mechanism by which mycorrhizal fungi improve P uptake is through more extensive soil exploration rather than a unique capacity to mobilize sources of P not available to plants (Sanders and Tinker 1971; Hayman and Mosse 1972).

While much of the P in the soil is inorganic, a large fraction may also be found in organic compounds. We have known for quite some time that roots of many plant species secrete phosphatases to help hydrolyze phosphate from such compounds, but evidence that arbuscular mycorrhizal fungi could do the same was obtained only recently (Joner et al. 2000; Koide and Kabir 2000). The significance of this ability is not currently appreciated.

The demonstration that arbuscular mycorrhizal fungi, free from contaminating microorganisms, could produce external phosphatases was possible only because of the availability of in vitro mycorrhiza cultures, but these are a comparatively recent development. In 1950, Harley wrote "Further advance must wait upon greater success in the isolation of the endophyte and in physiological work with them in culture". All attempts at independent culture of an arbuscular mycorrhizal fungus were unsuccessful. Clearly if research on the function of the extraradical mycelium were to proceed, another method would have to be developed. The first monoxenic (two-membered) mycorrhizas were produced by inoculating strawberry seedlings growing in test tubes containing various mixtures of loam soil, peat and charcoal sterilized by autoclaving or propylene oxide with surface-sterilized spores of *Glomus mosseae* (Mosse 1956). In several tests 25–60% of inoculated seedlings became mycorrhizal. Subsequent experiments with clover seedlings growing in various nutrient agar media yielded information on requirements for the establishment of monoxenic cultures and also on the effect of "helper bacteria" (*Pseudomonas* sp.) on entry of the fungus into the root (Mosse 1962). The development of monoxenic cultures meant that relatively large amounts of extraradical mycelium, attached to living host plants, could be produced in artificial culture. The gateway was thus opened to research on the physiology and genetics of the mycelium. Mosse's seminal research eventually led to experimentation with root organ cultures (Mosse and Hepper 1975; Mugnier and Mosse 1987) and to the eventual development in Quebec of in vitro transformed carrot root mycorrhizas. Research there was initiated by Bécard and Fortin (1988), who were the first to produce a root organ mycorrhiza that could sporulate. The basic method was later modified to produce even more fungal hyphae and spores in the absence of roots on one side of a split plate culture (St. Arnaud et al. 1996). Many other kinds of studies, both physiological and genetic, were made possible with the ability to culture a mycorrhiza in vitro. For example, this system allowed Bécard to demonstrate the need to form arbuscules in order to establish fungal biotrophy (Bécard and Piché 1989a). It also allowed him to show the synergistic positive effects of CO_2 and root exudates on fungal growth (Bécard and Piché 1989b). The positive effects of CO_2 are consistent with earlier studies of Mosse (1959a), who showed that spore germination of *Glomus mosseae* was stimulated by volatile substances created by other soil microorganisms growing from underlying soil particles. The historical development and research potential of mycorrhizal root organ cultures and the fundamental information they have already provided were reviewed recently (Fortin et al. 2002).

Earlier views on the putative pathogenicity of the symbiosis were sometimes based on the paucity of entry points, which would preclude any significant transfer of nutrients from fungus to plant. However, Bieleski (1973) calculated that with four hyphal entry points per millimeter root length and hyphae extending 20 mm from the root surface—both experimentally confirmed suppositions—P uptake per unit surface would be 60 times greater if P diffusion in the soil were limiting, and 10 times greater if it were not. In order for this to work, delivery of P from external to internal hyphae must occur. Cox et al. (1975) showed that polyphosphate granules existed within the hyphae, and the frequently observed cytoplasmic streaming was hypothesized to be the major mechanism for long distance transport of this polyphosphate (Cox et al. 1975, 1980; Callow et al. 1978; Cooper and Tinker 1981). It was later shown in an ectomycorrhizal fungus that the presence of polyphosphate granules can be an artifact of the fixation of tissues for microscopy and that the polyphosphate in vivo is actually soluble, at least in the ectomycorrhizal fungus *Pisolithus tinctorius* (Orlovich and Ashford 1993). Nevertheless, the early studies by Cox and colleagues suggested to them what we now consider to be the major mechanism for long distance P transport through the hyphae. The presence of alkaline phosphatase in the vacuoles of the fungi suggested a way to hydrolyze the polyphosphate prior to transfer to the host (Gianinazzi et al. 1979).

The next question was how the P could get out of the fungus and into root cells. Microscopic examination of roots usually reveals arbuscules in various stages of formation and decomposition, suggesting to some a role for the decomposition of arbuscules in nutrient transfer. In 1975, Woolhouse noted "there is a lingering implication in the literature of endotrophic mycorrhizas that the main exchange of materials, particularly from fungus to host, is dependent upon the deterioration and ultimate breakdown of the arbuscules." You will recall that the "sporangioles" observed long ago were arbuscules in various stages of decomposition. Now we take it for granted that arbuscule breakdown is not necessary for nutrient transfer. Bowen and Rovira (1968) may have been among the first to conclude that transfer of nutrients from fungus to host occurred across functional, intact arbuscules, followed by Woolhouse's model for active transmembrane exchange (Woolhouse 1975). Marx et al. (1982) presented what was perhaps the first biochemical evidence consistent with the role of the intact arbuscule in P transfer. They showed that the host plasmalemma, which invaginates around the arbuscular hyphae, had a very high ATP-ase activity (later shown to be H^+-ATPase; Gianinazzi-Pearson et al. 1991, 2000), suggesting the presence of active transport mechanisms. Kinden and Brown (1975) surmised from their scanning electron microscope study that while the large surface area of the arbuscule suggested that the intact structure was at least partly responsible for nutrient transfer, the short life span of the arbuscule suggested that breakdown of the arbuscule also contributed significantly to nutrient transfer. Nevertheless, Cox and Tinker (1976) concluded that arbuscule digestion was not necessary to account for the P transferred, based on calculated arbuscule lifespan, arbuscule volume and P concentration. Taken as a whole, the ultrastructural and physiological evidence suggests that most nutrient exchange occurs across the *living* host-fungus interface. Of course, that does not exclude the possibility that additional nutrient exchange occurs upon the death of the arbuscule.

Smith and Smith (1997) questioned whether arbuscules (alive or dying) are needed for P transfer, as intercellular hyphae may also be a site of P transfer (Ryan et al. 2003). However, plant P transporters, some of which are mycorrhiza specific, appear to be localized in cortical cells containing arbuscules (Rosewarne et al. 1999; Rausch et al. 2001; Harrison et al. 2002; Paszkowski et al. 2002).

Phosphorus is not the only mineral element taken up and transported to the host by mycorrhizal fungi. Gilmore (1971) may have been the first to point out that arbuscular mycorrhizal fungi could increase host Zn content, and Ross and Harper (1970) demonstrated the same for Cu.

Heap and Newman (1980) were perhaps the first to demonstrate the existence of hyphal linkages between roots of the same or different plant species. Ritz and Newman (1985) further showed that such linkages could transfer significant amounts of P from dying to living roots.

Fungal biotrophy and regulation of fungal growth

Although it is now generally accepted that arbuscular mycorrhizal fungi are biotrophic (Shachar-Hill et al. 1995; Solaiman and Saito 1997; Nakano et al. 1999) there was still lingering uncertainty about their carbon nutrition as late as 1967 (Nicolson 1967). However, in 1940 Peyronel had observed relationships between light and mycorrhization, and it had long been known that starch disappeared from cells with arbuscules. Peuss (1958) found that a reduction in light level (and thus presumably photosynthesis) severely decreased mycorrhization. Hayman (1973) also showed that light levels were positively correlated to mycorrhization, and particularly arbuscule formation (Hayman 1974). Using radioactive carbon, Ho and Trappe (1973) showed that recently produced photosynthate was transferred from host to fungus.

The quantitative regulation of fungal growth by the host through any mechanism will affect carbon transfer, and may even be partly mediated by the control of carbon transfer itself (Schwab et al. 1991; Koide and Schreiner 1992). Because plant P concentration (especially that of the roots; Koide and Li 1990) has also been shown to influence fungal growth, and because linkages between P and carbon transfer may exist (Woolhouse 1975; Schwab et al. 1991), plant P concentration was hypothesized to control fungal growth by influencing carbon transfer in various ways (Schwab et al. 1991). Long ago, Jones (1924) observed that plants growing in rich soil were usually less infected than those growing in poor soils. Many years later, in a series of articles, Daft and Nicolson (1966, 1969) investigated the relationships between mycorrhizal infection and soil P. They showed that mycorrhizal infection declined at higher P availabilities (Nicolson 1967; Daft and Nicolson 1969). Years later, results such as those led Hayman to comment on the apparent "self-regulatory" nature of the symbiosis (Hayman 1983), suggesting that when the cost to the host of supporting a mycorrhizal fungus exceeds the benefit, nature selects for physiological mechanisms of the host to reduce or eliminate the fungus. Recent biochemical studies summarized by Fortin et al. (2002) have provided a fascinating insight into pre-infection signals between roots and approaching fungal germ tubes that may also quantitatively control fungus growth and progression of the symbiosis. A somewhat overlooked area of research is the effect of root anatomical features in regulation of the symbiosis. Regulation of infection may be controlled in part by the anatomical features of the root such as suberization and air channel formation (Bonfante-Fasolo and Vian 1989; Brundrett and Kendrick 1990a, 1990b). Janse (1897), Demeter (1923) and Jones (1924) had made similar observations. The nature of the physiological control points that qualitatively determine whether a mycorrhiza becomes fully established is now being elucidated, in part, by the use of mutant plants. The first report of mutants that lacked the ability to form an arbuscular mycorrhiza occurred in 1989 (Duc et al. 1989). Studies of the factors that control fungal growth may eventually help us understand why some plant species are nonmycorrhizal or weakly mycorrhizal (Hirrel et al. 1978; Tester et al. 1987).

Applications

Research on the potential value of arbuscular mycorrhizal fungi in agriculture and land reclamation followed from the discoveries in the 1950s, 1960s and 1970s that they could substantially increase P uptake and plant growth under certain circumstances. However, the increasing number of observations that such fungi already exist in most agricultural soils led some to conclude that there would be little value in inoculation (Menge 1985). Khan (1972) may have been among the first to demonstrate that such a practice could be beneficial in some circumstances, but it would frequently prove to be uneconomic because of the large cost of inoculum production relative to the cost of phosphate fertilizer (Menge 1985). However, the practicality of inoculating soils that are inherently low in inoculum potential such as sterile citrus nursery beds (Menge et al.1977), sterile potting media, or soils that are highly disturbed may be greater. For example, the revegetation of disturbed lands, and the course of plant succession in such environments may be strongly influenced by inoculation with mycorrhizal fungi. Much of the pertinent literature on use of arbuscular mycorrhizal fungi in land reclamation was summarized in a publication edited by Williams and Allen (1984). The poem "Them Spore Pickers", written by Allen and included in that publication, is a real gem.

Potting "soils" used in the greenhouse are typically formulated from mixtures of materials such as peat moss, perlite and vermiculite, and thus lack mycorrhizal fungi. Inocula based on peat moss have been developed (Parent 1990), and these are capable of enhancing plant growth under some conditions (Ponton et al. 1990a, 1990b). However, it is not clear that the typical benefits of mycorrhizal fungi in increased phosphate uptake will always occur in potting media with low P adsorption (Biermann and Linderman 1983). Nevertheless, non-nutritional effects of mycorrhizal fungi, such as those on root branching (Berta et al. 1990, 1991), ethylene production (McArthur and Knowles 1992; Besmer and Koide 1999) or protection from pathogens (see below), may still be important.

Most inocula have been produced in pot cultures using soil mixtures (Wood 1985), but other technologies have been developed in the attempt to decrease costs and increase purity. These include nutrient film culture (Warner et al. 1985), aeroponics (Hung and Sylvia 1987) or expanded clay hydroponics (Dehne et al. 1987). There has been some notable research to develop practical on-farm inoculation production systems (Furlan 1993), and recent large-scale production of in vitro mycorrhizas may also increase the practicality of using inoculum (Adholeya 2003).

Relatively early on, researchers noted that different strains of the fungi produced different effects on plant growth (Mosse and Hayman 1971; Mosse 1972). Thus, the selection of superior strains of arbuscular mycorrhizal fungi that were notably effective on particular crops was an important activity for a time (Abbott and Robson 1982). However, the ability to displace indigenous strains, even those less effective than the introduced, superior strains, often proved to be difficult (Abbott et al. 1983). Moreover, what is "superior" for one crop may not be so for another subsequently planted crop, and what is superior under one set of environmental conditions may not be so under another (Menge 1985). Nonetheless, there have been some successes in at least the short-term establishment of effective strains following their inoculation in large-scale field trials (Owusu-Bennoah and Mosse 1979; Plenchette et al. 1981), but it must be admitted that we do not know how long such introduced strains persist.

Because of the costs of inoculum production and inoculum application, and the unpredictable consequences of strain selection, attention eventually turned to managing existing mycorrhizal fungal populations, such as by minimizing soil disturbance, reducing fallow periods, the application of chemical stimulants of the symbiosis, and the proper use of pesticides. As early as 1964 Clark found that physical disruption of the extramatrical mycelium reduced its ability to support good growth of seedlings of *Liriodendron tulipifera*, while inoculation with arbuscular mycorrhizal fungi overcame this. David Read and colleagues also drew attention to the significance of preexisting extramatrical mycelium to the infection of seedlings (Read et al. 1976). In 1975 Kruckelmann reported some important effects of various agricultural practices on the densities of mycorrhizal fungal chlamydospores. For example, the strong disturbance due to rotary hoeing significantly reduced spore density. In 1986, research performed in Canada showed that soil disturbance reduces mycorrhizal infection by disrupting the extramatrical mycelium, resulting in reduced P uptake, growth and yield in maize (O'Halloran et al. 1986). One of the benefits of minimizing tillage, therefore, is the reduced disruption of the extramatrical mycelium.

Thompson first reported in 1987 that long periods of fallow in Australian vertisols resulted in "long fallow disorder", the cause of which was an insufficiency in mycorrhiza inoculum. We now know that even short fallow periods, particularly in combination with harsh winter conditions, may also lead to a decline in inoculum potential that can be overcome by cover cropping (Kormanik et al. 1980; France et al. 1985; Dodd and Jeffries 1986; Galvez et al. 1995).

Some research focused on the discovery of root exudates, mostly phenolics, which could stimulate growth of the fungus and its entry into the root (Gianinazzi-Pearson et al. 1989; Nair et al. 1991; Siqueira et al. 1991; Bécard et al. 1992; Chabot et al. 1992; Kape et al. 1992). One of these phenolics, formononetin, has now been produced commercially and field tests have been performed (Elmer 2002).

The common use of pesticides in agriculture led some to determine their effects on the arbuscular mycorrhizal symbiosis. Depending on the crop and soil, some pesticides were found to have stimulatory, some to have depressive, and some to have essentially no significant effect on mycorrhizal fungi. Much of the literature on this subject was summarized by Smith (1978), Menge (1982) and Trappe et al. (1984).

As a natural reflection of their basic training in plant pathology, many researchers have investigated interactions among mycorrhizal fungi and phytopathogenic nematodes, viruses and fungi (summarized in Dehne 1982; Graham 1986). Many researchers have shown, for example, that mycorrhizal fungi can inhibit phytopathogenic fungi (Baltruschat and Schoenbeck 1972; Chou and Schmitthenner 1974; Dehne and Schoenbeck 1979). In some cases, the suppressive effect of mycorrhizal fungi on the development of disease is determined at the tissue level. For example, Dehn and Dehne (1985) showed that in the absence of mycorrhizal fungi, *Cochliobolus* infected all root tissues. When arbuscular mycorrhizal fungi were present, the pathogen was restricted to the epidermis and exodermis. Others have shown negative effects of mycorrhizal fungi on pathogenic nematodes (Fox and Spasoff 1972; Hussey and Roncadori 1977; Cooper and Grandison 1986). For the most part we do not know the mechanisms involved in such interactions (Azcón-Aguilar and Barea 1996b). For example, in some studies mycorrhizal infection increased phytoalexin activity (Morandi and Gianinazzi-Pearson 1985), whilst in other cases, it did not (Wyss et al. 1991).

Other non-nutritive effects of mycorrhizal fungi may be very important. In some respects, the early emphasis placed on the role of mycorrhizal fungi in promoting plant growth may have distracted us from another very important role they play as stabilizers of soil structure (Clough and Sutton 1976; Nicolson and Johnston 1979, Tisdall and Oades 1979, Miller and Jastrow 2000) and as integral components of a very diverse soil biota (Bethlenfalvay and Schüepp 1994; Franke-Snyder et al. 2001).

Ecology

The goal of the ecologist is to study organisms in natural ecosystems without necessarily any desired practical outcome. Although the goals of the ecologist and the agriculturist are thus different, they are often complementary, and research in ecology has great potential to lead to advancement in agriculture. Initial ecological research on arbuscular mycorrhizas led to the realization that the symbiosis was widespread, both in terms of the number of plant species involved, and in terms of the number of ecosystems possessing it. For example, Jones (1924) found that a diversity of soils across the United States supported arbuscular mycorrhizal plants.

The autecology of the arbuscular mycorrhizal fungi has been the subject of research for many years. For example, Lohman (1927) investigated the effects of soil pH on mycorrhization, as did Peuss (1958) and Porter et al (1987), among many others. Many have investigated the effects of temperature (Furlan and Fortin 1973; Hayman 1974) and soil moisture (Reid and Bowen 1979) on the symbiosis, but Jones (1924) was probably the first to investigate these relationships. The effects of freezing or drying on survival of the fungi do not appear to have been examined until relatively recently (Jasper et al. 1989; Addy et al. 1994, Kabir et al. 1997; Klironomos et al. 2001). The nature of spore dormancy and the environmental factors that overcome it have been investigated by many authors through the years (Mosse 1959a; Siqueira et al 1985). Some authors have noted that mycorrhiza inoculum potential varies with soil depth (Schwab and Reeves 1981; Koide and Mooney 1987), but this had already been noted years earlier (Jones 1924). Nicolson (1959) and Mosse (1959a) described in some detail the dimorphic nature of the soil mycelium, and the ecological relevance of this has been discussed by Read (1992).

Hyphal anastomoses, which are potentially very important to the ecology of the fungi, were noted early on (Gerdemann 1955b; Mosse 1959b, 1963). Mosse indicated that anastomoses provide the possibility for "hybridization" or exchange of genetic material, which has been confirmed recently (Giovannetti et al. 2001). This provides a means to maintain adaptability and diversity in otherwise apparently asexual fungi. Anastomoses may also permit resource transfer among individual fungi. The fact that different species do not form anastomoses with each other (Giovannetti and Sbrana 2001) indicates that the benefits of the physiological integration among individuals of a single species are not afforded between species.

The early observations that plant species differed in their response to mycorrhizal fungi (Lohman 1927; Baylis 1970, 1972b) and that some plant species were nonmycorrhizal, led to the hypothesis that the fungi could help to structure natural plant communities. Indeed, mycorrhizal fungi may influence the course of plant succession (Nicolson 1960; Janos 1980) and the relative competitive abilities of host plants (Crush 1974; Fitter 1977; Hall 1978). In some cases, antagonistic interactions between arbuscular mycorrhizal fungi and some plant species may also serve to exclude these plants from mycorrhizal plant communities (Allen et al. 1989; Francis and Read 1984, 1985). Mycorrhizal fungi may also influence plant communities by affecting species evenness (Grime et al. 1987; O'Connor et al. 2002) or species richness (Gange et al. 1990).

Although there is no evidence of strict host-fungus specificity with arbuscular mycorrhizas (but see Helgason et al. 2002), the composition of the mycorrhizal fungal community has the potential to both influence (van der Heijden et al. 1998) and be influenced by (Hetrick and Bloom 1983; Anderson and Liberta 1985; Bever et al. 1996) plant community composition. These interactions clearly have relevance to agroecosystems, particularly where crop rotations or intercropping are involved.

Interactions between mycorrhizal fungi and other organisms occur and may influence the function of the fungi. While grazing of mycorrhizal hyphae by fungivorous collembola can reduce host plant P uptake (Warnock et al. 1982; McGonigle and Fitter 1988) collembola may also disseminate mycorrhizal fungal propagules (Klironomos and Moutoglis 1999). Rodents may also be agents of dispersal as *Endogone* spores were shown to remain viable after passage through their alimentary tracts (Godfrey 1957). Some of the interactions among mycorrhizal fungi and other soil organisms have been summarized by Azcón-Aguilar and Barea (1992) and Fitter and Sanders (1992). Electron microscopy has revealed the unexpected presence of large numbers of bacteria-like structures (sometimes referred to as bacteria-like objects or BLOs) within spores and hyphae of arbuscular mycorrhizal fungi (Mosse 1970; MacDonald et al. 1982; Scannerini and Bonfante 1991). We now know that these truly are bacteria that are apparently obligate symbionts of the fungi. Some of the bacteria are being characterized using DNA-based methods and can represent 40% of total spore DNA (Bianciotto et al. 1996, 2003). Their significance to the biology of the fungus has yet to be worked out.

The discovery that benomyl could be effective against arbuscular mycorrhizal fungi led to its use in several ecological studies, particularly by Fitter and his associates (Fitter 1986; Carey et al. 1992; Newsham et al. 1995; Merryweather and Fitter 1996) in which they described the effects of mycorrhizal infection on seed production, and interactions among mycorrhizal fungi and plant pathogenic fungi. Koide and his associates have also shown significant effects of mycorrhizal fungi on plant fitness, both in terms of individual plant fecundity, seed quality, and plant population dynamics (summarized in Koide 2000; Koide and Dickie 2002).

In 1996 Wright and Upadhyaya described the existence of a novel protein produced by arbuscular mycorrhizal fungi. This compound came to be known as glomalin. At least some forms of it appear to be comparatively recalcitrant, thus allowing high concentrations to build up in the soil. Moreover, it may serve a role in soil aggregation and it represents a relatively large pool of carbon and nitrogen (Miller and Jastrow 2000).

Thus it is clear that mycorrhizal fungi are important components of natural ecosystems, and that they can have strong influences on plant community composition and ecosystem function. Some of these influences have been summarized by Hart and Klironomos (2002) and by Bever et al. (2002).

On becoming "mycorrhizologists"

The study of arbuscular mycorrhizas has been carried out through the years by a disparate group of mycologists, botanists, plant pathologists, plant physiologists, plant anatomists and plant ecologists, all coming to the mycorrhiza from different points of view. There is now movement to form an International Mycorrhiza Society, but even without a formal organization past researchers did not necessarily work in complete isolation from each other. The mycorrhiza research community was unified by two major factors. First a great deal of research on the arbuscular mycorrhiza during the middle part of the twentieth century saw the light of publication through a relatively small number of journals. Second, increasingly inclusive international conferences have been regularly organized. At one such meeting, as a joke, Harley proposed the name "mycorrhizast" for researchers of the symbiosis. This was taken seriously by some for a period. However, to be consistent with other disciplines such as physiology or pathology, we were all reborn with the invention of the more etymologically justifiable name "mycorrhizologist"!

Among the oldest journals to regularly publish research on mycorrhizas was the *Transactions of the British Mycological Society*. The *Transactions* were published between 1896 and 1989, when the journal was renamed *Mycological Research* in order to reflect its already well-established international readership. The *New Phytolologist*, originally subtitled *A British Botanical Journal*, was founded in 1902 and was first edited by the plant ecologist, Arthur Tansley. The first reference to arbuscular mycorrhiza in the *New Phytolologist* was a note written by Blackman (1903) about observations made by Shibata (1902). The journal also published an early paper on endotrophic mycorrhiza by Rayner (1916). Early on, the *New Phytolologist* published several important reviews of the mycorrhizal symbiosis. For example, in 1926 and 1927 it reprinted, in its entirety, the book on the mycorrhiza written by Rayner (1926–1927. There appeared in 1936 another early review on mycorrhiza written by Burges. In 1950 the *New Phytolologist* published a review by Harley of endotrophic mycorrhizas, which included the vesicular-arbuscular, orchid and ericaceous mycorrhizas. In 1962 Harley became an editor for the *New Phytolologist* and was later joined by two former students, Smith and Lewis (Lewis and Ingram 2002). Together, they continued the tradition already established at the *New Phytolologist* of serving as an outlet for research on plant symbioses and, in particular, the mycorrhiza. Indeed, it would be difficult to overestimate the historical importance of the *New Phytolologist* to the study of mycorrhiza.

Today important research continues to be published in these journals and others that have established their own traditions as outlets for mycorrhiza research such as *Mycologia* (established 1909), *Canadian Journal of Botany* (established 1929), *Plant and Soil* (established 1949), *Soil Biology and Biochemistry* (established 1969), *Applied and Environmental Microbiology* (established 1976) and, of course, *Mycorrhiza*, which was established in 1991 as the only international journal devoted entirely to the study of mycorrhiza. Its establishment and subsequent growth are, in part, consequences of the vitality of our field.

The publication of books that summarize the state of knowledge and offer the perspectives of their authors has also done much to add academic (if not, literal) heft to our discipline. Probably the earliest such book was that written by Rayner (1926–1927). Harley authored a book entitled *The Biology of Mycorrhiza* in 1959, and its second edition in 1969. These were followed by other important books including *Mycorrhizal Symbiosis* (Harley and Smith 1983), and its second edition (Smith and Read 1997). The first book devoted solely to arbuscular mycorrhiza was edited by Powell and Bagyaraj (1984). Other publications are particularly noteworthy as excellent compilations of methods: Schenck (1982), Brundrett et al. (1994, 1996) and Varma (1998).

In the days before faxes and electronic mail messages, and even before international phone services were economical, meetings at which scientists could discuss research face-to-face also played an important role in unifying the arbuscular mycorrhiza research community. The first international meeting devoted entirely to mycorrhiza of which we are aware, “Mycorrhiza, Internationales Mykorrhizasymposium”, occurred in 1960 in Weimar, in the former German Democratic Republic. The proceedings of this conference (Rawald and Lyr 1963) were published in German and, unfortunately, few libraries possess a copy of them. Nicolson was one of a few to present research on the arbuscular mycorrhiza, which was, at the time, the stuff of the odd specialist. You will recall that Harley did not refer to the study of arbuscular mycorrhiza as a “reputable pursuit” until 9 years after this conference!

Nine North American Conferences on Mycorrhizae (NACOM) were held from 1969 (Hacskaylo 1971) to 1993 (Peterson and Schelkle 1993). The meetings were held, respectively, in Illinois, Oregon, Georgia, Colorado, Quebec, Oregon, Florida, Wyoming, and Ontario. Initially these conferences included little or nothing about arbuscular mycorrhizas, but this was eventually remedied. And, despite the name, these conferences became progressively intercontinental. Indeed, from 1969 until 1985 NACOM was the only regular international gathering of mycorrhiza researchers, and thus served a critical function in stimulating research.

The second formal European meeting devoted to research on mycorrhiza, and much of it arbuscular mycorrhiza, “Endomycorrhizas”, was held in 1974, in Leeds (UK). Its proceedings (Sanders et al. 1975) were made more available than those from the Weimar meeting, and were published in English. This publication did much to popularize arbuscular mycorrhiza as a legitimate scientific pursuit. Although small by comparison to recent international meetings (there were only 70 listed participants), one advantage certainly was the ability to fit nearly all the participants into a single photograph!

The meetings in Weimar and in Leeds were followed by a series of European Symposia on Mycorrhizas held every 3 years beginning in 1985. The first was held in France (Gianinazzi-Pearson and Gianinazzi 1986), the second in Czechoslovakia (Mejstrik et al. 1990), the third in England (Read et al. 1992), and the fourth and final meeting in Spain (Azcón-Aguilar and Barea 1996a). These meetings did much to stimulate research in the areas of physiology, biochemistry, genetics and ecology. Another international symposium was held in Australia in 1992 (Robson et al. 1994). To minimize the duplication of effort and to further promote international cooperation, organizers decided to consolidate the NACOM, the European Symposia, and other international efforts into the current International Conference on Mycorrhiza (ICOM). Despite this fusion, there remains one interesting difference between conferences held in North America and Europe. North American conferences have been about “mycorrhizae” while European and Australian conferences have been about “mycorrhizas”, an observation noted by Nicolson in 1967. A simple solution to end this confusion might be to use “mycorrhiza” as both the singular and the plural, as many of us already have done anyway.

International collaborations have done much to foster a sense of community among mycorrhiza researchers. In this respect the Europeans are leading the way. Initiatives such as the COST Actions over the last 12 years have been very important in funding innovative research and in fostering collaborations among researchers in several nations (Gianinazzi and Schüepp 1994; Gianinazzi et al. 2002). This model for large-scale collaboration is likely to lead to large advances in the field as researchers from around the world are united in common goals.

Conclusion

The discovery of the arbuscular mycorrhiza was made more than 100 years ago. Early studies were purely descriptive, but it is amazing to review the sophisticated conclusions that were drawn despite the inability at the time to perform experiments. In some cases those conclusions were correct and recently we have merely been refining a wheel invented years ago. In other cases, notably the effects of mycorrhizal fungi on plant growth and nutrient uptake, experimentation was necessary to arrive at the correct conclusion, and this occurred relatively recently. Current researchers thus owe a debt of gratitude to past generations of researchers, most of whom are removed by only a generation or two. As one studies the “old” papers, one might have a tendency to marvel at what was not known in just the recent past. However, what is more surprising and encouraging is what had been logically deduced with only a limited set of research tools and modest research budgets. It seems that in many cases the technological limitations of yesteryear were more than compensated for by imagination and mental exertion. If we continue to question, imagine and deduce as well as some of the past researchers did, we will make tremendous progress given the ever-increasing sophistication of the available research tools.

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